# Effects of selective logging on tree species diversity and composition of Bornean tropical rain forests at different spatial scales

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**Word count:** 5,972

**Abstract** Reduced-impact logging (RIL) is known to be beneficial in biodiversity conservation, but its effects on tree diversity remain unknown. Pattern of tree diversity following disturbance usually varies with spatial scale of sampling (i.e. plot size). We examined the impacts of RIL on species richness and community composition of tree species at different spatial scales, and the scale (plot size) dependency of the two metrics; species richness vs. community similarity. One 2-ha and three to four 0.2-ha plots were established in each of primary, RIL and conventionally logged (CL) forest in Sabah, Malaysia. Species richness (the number of species per unit number of stems) was higher in the RIL than in the CL forest at both scales. The relationship between species richness and logging intensity varied with plot size. Species richness was greater in the RIL than in the primary forest at the 2-ha scale, while it was similar between the two forests at 0.2-ha scale. Similarly, species richness in the CL forest demonstrated a greater value at the 2-ha scale than at the 0.2-ha scale. Greater species richness in the two logged forests at the 2-ha scale is attributable to a greater probability of encountering the species-rich, small patches that are distributed heterogeneously. Community composition of the RIL forest more resembled that of the primary forest than that of the CL forest, regardless of plot size. Accordingly, species richness is a scale-dependent metric, while community similarity is a more robust metric to indicate the response of tree assemblage to anthropogenic disturbance.

**Keywords** Borneo; forest heterogeneity; non-metric multi-dimensional scaling (NMDS); PERMANOVA; species-accumulation curves

## Introduction

Forests degraded due to anthropogenic disturbances are rapidly expanding in area in the tropics (Asner et al. 2005; Wright 2005). Degraded tropical forests usually have higher species richness than monocultural plantations and agricultural lands (Gibson et al. 2011, Lawton et al. 1998). On the other hand, strictly protected areas that are expected to conserve biodiversity are rather limited in area (Rodrigues et al. 2004), leading to a growing interest in the conservation value of degraded tropical forests (Berry et al. 2010, Edwards et al. 2010). A key driver of forest degradation in Southeast Asian tropics is unregulated selective logging, which often damages more than 50% of the original forest biomass, and causes surface-soil disturbance (Bertault and Sist 1997; Cannon et al. 1994; Pinard and Putz 1996; Putz et al. 2008a; Sist et al. 1998). Understanding the responses of biodiversity to selective logging in the tropics is crucial for predicting and managing biodiversity in our rapidly changing global environment.

To mitigate the detrimental impacts of selective logging on forests, “reduced-impact logging” (RIL) has recently been applied to some of natural production forests in the tropics (Kleine and Heuveldop 1993; Lagan et al. 2007; Putz et al. 2008a). RIL is a modification of selective logging, including pre-harvest inventory, mapping of all canopy trees, directional felling, liana cutting and planning of skid trails, log decks and roads. In comparison with unregulated conventional logging (CL), RIL is beneficial not only in maintaining future crop trees (Peña-Claros et al. 2008; Rockwell et al. 2007) and forest biomass (Bertault and Sist 1997; Johns et al. 1996; Miller et al. 2011; Pinard and Putz 1996; Putz et al. 2008b; Sist et al. 1998),

but also in biological diversity, such as dung beetles (Davis 2000), flying insects (Akutsu et al. 2007), soil macrofauna (Hasegawa et al. 2006) and forest-dwelling vertebrates (Imai et al. 2009). Many other taxa, such as ants, arachnids, bats, birds, fishes and animals, also are not adversely affected by RIL (Azevedo-Ramos et al. 2006; Bicknell and Peres 2010; Castro-Arellano et al. 2007; Dias et al. 2010; Edwards et al. 2012; Felton et al. 2008; Presley et al. 2008; Samejima et al. 2012; Wunderle et al. 2006). However, the effects of RIL on tree species diversity of tropical rain forests remain largely unknown, despite that the diversity of trees is fundamental to the structure and functions of the forests. The diversity of trees may also determine the diversity of other taxonomic groups, because trees provide resources and habitat structure for dependent species.

To date, only three studies have examined the effects of RIL on tree species diversity (Foody and Cutler 2003; Medjibe et al. 2011; Webb and Peralta 1998). However, two studies compared tree diversity of RIL with that of primary forest (Medjibe et al. 2011; Webb and Peralta 1998), and only one study compared tree diversity of RIL with that of both primary and CL forest by using quite a small (0.05 ha in area) plot (Foody and Cutler 2003). Given that widespread commercial logging of high-value timber in the tropics still rely mainly upon conventional techniques (Blaser et al. 2011), comparison of logging impacts on tree diversity between RIL and CL is urgently needed.

Tree species richness (number of tree species at a single site) in selectively logged forests may vary depending on the spatial scale of sampling (Dumbrell et al. 2008; Hamer and Hill 2000; Hill and Hamer

2004). Selectively logged forests consist of a mosaic of patches affected by different intensities of disturbance, such as remnant stands, gaps due to harvesting and road construction, and regenerating patches with varying successional stages. A small plot can encounter only one or a few patch types within a heterogeneous logged-over forest. On the other hand, a large plot is potentially able to encounter all different patch types within the forest. Because logging creates new habitats for the species not found in a primary forest, deploying a large plot overestimates species richness in a logged-over forest. Accordingly, plot size, which determines the number of different patch types encountered in a given area, can in turn affect species richness in that area. However, previous studies assessing tree species richness in selectively logged forests have used either small (mostly less than 0.2 ha in area) or large plots (1 ha in area in a few studies; Berry et al. 2008; Chua et al. 1998; Kirika et al. 2010; Medjibe et al. 2011; Ouédraogo et al. 2011, Souza et al. 2012). Deploying both small and large plots is necessary to reliable evaluation of logging impacts on tree species richness.

The ideal metric of biodiversity must be independent of spatial scale of sampling (Chazdon et al. 1998). Sheil and Burslem (2003) reported that tree species richness in tropical forests following habitat disturbance varied with spatial scale. On the other hand, community similarity (difference of community composition between sites) is receiving increasing attention as a useful metric to assess the effects of forest managements on biodiversity, rather than species richness (Barlow et al. 2007; Su et al. 2004). Despite that, no assessment of the scale-dependent response of tree community similarity to habitat disturbance has yet been conducted. Understanding the

scale dependency of the two major metrics following disturbance can improve the interpretation of the outcome of tropical biodiversity studies, in which sampling size and evaluation metrics largely differ among different studies.

We established one 2-ha and three to four 0.2-ha plots in each of primary, RIL and CL forest in Bornean lowland tropical rain forests to examine the effects of RIL on tree species richness and composition at different spatial scales. We also compared the scale (plot size) dependency of the two metrics (species richness vs. community similarity) to consider which metric is more appropriate for evaluation of the forest-management effects on tropical biodiversity.

## Material and methods

### Study site

This study was carried out in Deramakot Forest Reserve and Tangkulap Forest Reserve in Sabah, Malaysia (5°14-30'N, 117°11-36'E). The mean annual temperature of the area is 27°C and the mean annual precipitation is *c*. 3500 mm, with little seasonal variation. The region is characterized by Tertiary sedimentary rocks. The altitude in the reserves is between 20 and 300 m asl. The vegetation is a mixed dipterocarp lowland tropical rain forest. Deramakot (551 $km^2$) and Tangkulap (275 $km^2$) are located adjacent to each other.

Deramakot and Tangkulap were originally licensed for logging starting in 1956 and the 1970s, respectively. Subsequently, conventional logging commenced there (Sabah Forestry Department 2005). During 1959-1968, timber, with a mean volume of 109 $m^3$/ha, was harvested in

Deramakot (Sabah Forestry Department 2005). In 1989, Deramakot was chosen by the Sabah State Government as a model site to develop a sustainable forest management system and all logging activities were suspended thereafter. A new management system with RIL was implemented in 1995. Deramakot is now divided into 135 compartments of varying sizes (approx. 500 ha each), and about two to four compartments are harvested annually using RIL with a planned rotation period of 40 yr (Lagan et al. 2007). 17 of these compartments (3,473 ha in area) are reserved for conservation (not to produce logs).

Based on the guidelines of RIL, all harvestable trees must be measured before harvesting and located on a detailed map and appropriate routes for skidders are designed to minimize the damage to non-target trees. The trees harvested are limited to those in the range of 60-120 cm diameter at breast height (dbh), and trees that are near streams, on steep terrain, with hollows, or of fruiting species for wildlife are excluded from harvesting. A compartment will be harvested only when the harvestable timbers exceed 25 $m^3$/ha. Tangling lianas are cut before harvesting and targeted trees are harvested with a directional felling technique. Harvesting and road construction cease during periods of heavy rainfall to reduce soil erosion. Gap size of each harvesting must be less than 0.1 ha. Dipterocarpaceae is one of the major targeted tree families for harvesting. In Deramakot, a total of 24,934 trees (2.36 trees /ha) with a volume of 145,399 $m^3$ (13.74 $m^3$/ha) were harvested during 1995-2006 (Samejima et al. 2012).

Tangkulap Forest Reserve was repeatedly logged using a conventional logging technique until 2001, when the government suspended all logging

activities. There are no reliable statistics for the log production in Tangkulap. According to the analysis of logging history in the two reserves using Landsat satellite data (Imai et al. 2009), much heavier logging have occurred in greater areas in Tangkulap compared with Deramakot during 1985-2002. This difference of degradation status between Deramakot and Tangkulap resulted from the differences of the two logging methods (i.e. RIL and CL) and harvested volume between the two reserves. We used these forests as a model site to examine the impacts of RIL on species richness and community composition of tree species at different spatial scales, and the scale (plot size) dependency of the two metrics; species richness vs. community similarity.

Vegetation survey

Eleven research plots of 0.2 ha were established in Deramakot and Tangkulap during May 2003-March 2005 (Seino et al. 2006). In Deramakot, four plots were established in a primary forest located within the conservation area. Conventional logging method has been applied even in the current conservation area until the 1980s, and there are still evidences of the past logging activities (e.g. old bulldozer paths, old stumps, and absence of emergent trees) in the vicinity of our plots. However, we considered our four plots are in unlogged patches of primary forest, because of the absence of any evidence of past logging activities within the plots. In Deramakot, we also set up four plots in the forest logged by RIL during 1995-2000. In Tangkulap, three plots logged by CL were established. The three CL plots were once logged before 1988, and again logged during 1995-1999, based on the observation of Landsat scenes (Aoyagi R. pers. comm.). Thus, the two logged

forests were logged during the similar period; RIL and CL forest were logged 5-13 and 5-10 yr before our investigation, respectively. Eleven 0.2-ha plots were laid out primarily as 100 × 20 m. Three out of the four plots in primary forest and one out of the three plots in CL forest were laid out as 50 × 40 m, because of the limited availability of gentle topography. Mean (± SD) distances among the 0.2-ha plots are 435 ± 209, 1130 ± 646 and 756 ± 175 m for primary, RIL and CL forest, respectively. During November 2006-February 2008, we enlarged one representative 0.2-ha RIL plot and one representative 0.2-ha CL plot to 2 ha in area (200 × 100 m). We additionally established a new 2-ha plot in primary forest, because the four 0.2-ha primary plots are in small patches of residual forest and therefore cannot be enlarged without including degraded patches. Each plot consists of 10 × 10-m subplots.

All trees ≥10 cm dbh were measured in each plot. We also established a hundred 5 × 5-m plots within a 2-ha plot (allocated alternately to each 10 × 10-m subplot), and measured dbh of small trees with 5-10 cm dbh. Buttressed trees were measured at well above (*c*. 50 cm) protrusions. All trees were identified by botanical experts of the Herbarium, Forest Research Centre, Sabah Forestry Department, Sandakan. Voucher specimens were collected from the trees that could not be identified in situ. Specimens taken were compared with herbarium collections. Samples that could not be identified to species were distinguished as morphospecies.

Plot shape may affect tree species richness, because a rectangular plot may sample a greater number of species than a square plot of the same area (Condit et al. 1996). However, when we tested the effects of plot shape (100 × 20 m vs. 50 × 40 m) using subplots within a 2-ha plot, the mean

number of tree species ≥10 cm dbh did not significantly differ between ten 100 × 20-m subplots and ten 50 × 40-m subplots (Student's *t*-test, $P > 0.5$ for all, only 1.1-1.9 species greater in 100 × 20-m subplots). This is probably because the aspect ratio of our study plots was relatively low {only from 1.25 (50 × 40 m) to 5 (100 × 20 m)}. We therefore suggest that the use of different plot shapes does not affect tree species richness in our study.

Data analysis

*Above-ground biomass*

Above-ground biomass (AGB) was estimated according to the allometric equation obtained by Chave et al. (2005) as:

$$AGB = \rho \times \exp(-1.499+2.148\ln(D)+0.207(\ln(D))^2-0.0281(\ln(D))^3)$$

where $D$ is dbh (cm) and $\rho$ is the wood-specific gravity (g/cm$^3$). We obtained the wood-specific gravity $\rho$ for the observed species/genera from various sources (Lemmens et al. 1995; Oey 1951; Soerianegara and Lemmens 1993; Sosef et al. 1998). In cases, where a range of wood density values were reported, we used a median value. Where wood density data were unavailable for a species, the average across all species in that genus was applied (see Baker et al. 2004; Slik 2006). In the few cases, where trees could not be identified at the genus level or where no literature record was available, we used the mean wood specific gravity of that plot.

*Forest heterogeneity*

To evaluate the forest heterogeneity within a 2-ha plot in each forest type,

we calculated a commonly-used measure of β-diversity (Whittaker 1960) within a 2-ha plot:

$$\beta = \gamma / \alpha$$

We calculated the number of species at the scale of 40 × 50 m within each of the 2-ha plots (i.e. ten 0.2-ha subplots by sequentially shifting 40 × 50-m quadrat per 2-ha plot), and obtained β by dividing the total number of species in each 2-ha plot (γ) by the mean number of species per 0.2-ha subplots (α).

*Community similarity*

We tested the differences in tree community composition among forest types using ordinations and permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). The Chao dissimilarity (distance) function and the relative basal area of each species in eleven 0.2-ha plots ($n$ = 11) and three 2-ha plots separated at the scale of 40 × 50 m within each of the 2-ha plots ($n$ = 30) were used to calculate the distance matrix. The PERMANOVA used the “adonis” procedure in the vegan package in R. Ordinations were plotted with non-metric multidimensional scaling (NMDS) using the vegan’s “metaMDS” procedure.

*Species richness*

We estimated the number of tree species by using rarefaction, which is used to calculate the number of species expected in a subsample selected at random from a total sample (Gotelli and Colwell 2001; Magurran 2004). We ran 100 randomizations using the data of the number of trees ≥10 cm dbh for

each species at 10 × 10-m subplots by EstimateS ver. 8 (available online at http://viceroy.eeb.uconn.edu/estimates) to produce species-area curves. The species-individual curves were obtained by converting the cumulative area to cumulative numbers of individuals. Estimated number of species for 70 stems in the 0.2-ha plots and for 850 stems in the 2-ha plots were separately calculated by interpolation from the species-individual curves; 70 and 850 were the number of individuals in the site with the smallest total number of individuals at each plot size.

Differences in vegetation properties (stem density, basal area, AGB, observed and estimated number of species) among forest types were tested by an analysis of variance (ANOVA). When the ANOVA $P$ value was $< 0.05$, the Tukey-Kramer *post hoc* test was performed to determine which pairs of means differ significantly.

*Scale dependency of the two metrics*

To examine the scale dependency of the two metrics, we tested which metrics (species richness and community similarity) better correlated with AGB at both 0.2-ha and 2-ha scales. Estimated AGB in each plot was considered as a surrogate of the degree of forest degradation. Estimated number of species in each plot was used as an index of species richness, because it can compare expected species richness between data of different sample sizes (Gotelli and Colwell 2001; Magurran 2004). NMDS axis 1 score in each plot was used as an index of community similarity.

Unfortunately, we established only one 2-ha plot per forest type due to impenetrability in our study site. However, the lack of replicates is not

critical in this analysis because we applied a linear model.

## RESULTS

### Forest structure

Stem density in 0.2-ha plots tended to be lower in CL than in the other two forests ($P < 0.1$), but did not differ between primary and RIL forest (Table 1). Stem density in 2-ha plots decreased with increasing logging intensity (Table 1). Densities of trees ≥60 cm dbh in 0.2-ha plots and trees with 5-10 cm dbh in 2-ha plots were lower in CL than in the other two forests (Fig. 1, $P < 0.05$ for both).

In 0.2-ha plots, AGB, maximum dbh and total basal area were lower in CL than in the other two forests, but did not differ between primary and RIL forest (Table 1). These structural properties showed a similar pattern also in 2-ha plots to that shown in 0.2-ha plots.

### Community similarity and forest heterogeneity

Dipterocarp species dominate primary and RIL forest, while pioneer species (mostly *Macaranga* spp.) were abundant in CL forest (Table 1). Community composition consistently differed between CL and the other two forests at both 0.2-ha (PERMANOVA, $P < 0.05$) and 2-ha scales ($P < 0.001$) (Table 2). While community composition of RIL forest also differed from that of primary forest at 2-ha scale ($P < 0.001$), it did not differ from that of primary forest at 0.2-ha scale ($P > 0.05$). Primary and CL forest were plotted at the opposite extremes along the NMDS axis 1 consistently at both scales (Fig. 2a,b). RIL forest was plotted at similar positions with primary

326 forest at 0.2-ha scale (Fig. 2a) while at an intermediate position at 2-ha
327 scale (Fig. 2b).
328 Forest heterogeneity within a 2-ha plot, measured with Whittaker's
329 β-diversity, increased with increasing logging intensity (4.1, 4.6 and 4.8 in
330 primary, RIL and CL forest, respectively).
331
332 Species richness
333 We recorded 1324 stems of 360 species in 0.2-ha plots and 2992 stems of
334 544 species (3614 stems ≥ 5 cm dbh of 589 species) in 2-ha plots. Observed
335 number of families and genera were lower in CL than in the other two
336 forests in 0.2-ha plots, while it did not largely differ among forest types in
337 2-ha plots (Table 1). Observed number of species per unit area was lower in
338 CL than in the other two forests, but did not differ between primary and RIL
339 forest, regardless of plot size and tree size class (Table 1, Fig. 3a-c,g-j).
340 Species richness (estimated number of species) in 0.2-ha plots was
341 also lower in CL than in the other two forests (Table 1). Species richness in
342 2-ha plots was greater in RIL, intermediate in primary, and lower in CL
343 forest. Species richness of primary forest was 1.6 times greater at 0.2-ha
344 scale (50.1 vs. 31.1 species), while only 1.06 times greater at 2-ha scale
345 than that of CL forest (257 vs. 243 species). Such higher species richness of
346 the two logged forests at 2-ha scale compared at 0.2-ha scale is due to the
347 difference in species richness of small trees between 0.2-ha and 2-ha scale.
348 In 2-ha plots, species richness of trees with 5-20 cm dbh did not differ
349 between primary and CV forest (Fig. 3m,n), and that with 10-20 cm dbh was
350 rather higher in RIL than in primary forest (Fig. 3m).

Scale dependency of the two metrics

A significant relationship between species richness and AGB (as the degree of forest degradation) was obtained at only one out of the three plot designs (i.e. replicated 0.2-ha plots) (Fig. 4a). By contrast, there was a consistent linear relationship between NMDS axis 1 scores (as community similarity) and AGB irrespective of plot design (Fig. 4d-f).

## DISCUSSION

Species richness in RIL forest was consistently higher than that in CL forest at both spatial scales, and rather higher than that in primary forest at 2-ha scale. Conventional logging in Tangkulap has caused a greater disturbance, which have led to the loss of late-successional species. Logging following the RIL guidelines in Deramakot extracted a reduced volume of timber and reduced collateral damages to the residual stands (Lagan et al. 2007). Such efforts may create favorable habitats for pioneer species, while maintain the late-successional species, leading to the greater species richness in RIL than in the other two forests. This may correspond with the intermediate disturbance hypothesis (Connell 1978), which predicts local species diversity to be maximal at an intermediate level of disturbance, due to the coexistence of late-successional and pioneer species. Accordingly, RIL does not appear to reduce tree species richness substantially, nor does it promote the prolific colonization of pioneer species.

Relationships between tree species richness and logging intensity varied with plot size. There was no difference in species richness between primary and RIL forest at 0.2-ha scale, but rather higher richness in RIL

than in primary forest at 2-ha scale. Species richness of primary forest was 1.6 times greater at 0.2-ha scale, but only 1.06 times greater at 2-ha scale than that of CL forest. Logged forests consist of both patches with low species richness (due to the degradation or the dominance of a few pioneer species recruited) and patches with relatively high species richness (due to the coexistence of late-successional and pioneer species at small size class). In degraded forest landscapes, the latter patches may occupy a small area and be distributed heterogeneously. Probability of encountering such patches with high species richness will decrease when sampled with smaller plots. This is one major reason why the two logged forests showed relatively higher species richness at 2-ha scale compared at 0.2-ha scale.

Previous studies have demonstrated inconsistent responses of tree species richness to selective logging, with unchanged (Bischoff et al. 2005; Foody and Cutler 2003; Hall et al. 2003; Kirika et al. 2010; Medjibe et al. 2011; Slik et al. 2002; Verburg and van Eijk-Bos 2003), decreased (Brearley et al. 2004; Gutiérrez-Granados et al. 2011; Makana and Thomas 2006; Okuda et al. 2003), and increased (Berry et al. 2010; Cannon et al. 1998; Plumptre 1996) richness following logging. Most studies used a single plot size, and compared species richness between unlogged and logged forests without the variation of logging intensity (but see Kirika et al. 2010; Molino and Sabatier 2001; Verburg and van Eijk-Bos 2003). Selective logging actually has a wide variation in the volume of timber extracted and the severity of damage caused by the removal of individual trees and road construction (Cannon et al. 1994). Our results indicate that responses of tree species richness to logging intensity can covary with plot size. These

two uncontrolled factors (logging intensity and plot size) among different studies may be the possible reasons for the inconsistent responses of tree species richness to selective logging.

Unlike species richness, community composition of RIL forest more resembled that of primary forest than that of CL forest regardless of plot size. Therefore, community similarity consistently showed a linear relationship with the degree of forest degradation irrespective of plot design (Fig. 4). Community similarity is a sensitive and consistent metric to evaluate the effects of logging on tree assemblage, rather than species richness per se, which inevitably combines the responses of two contrasting regeneration guilds (pioneer and late-successional species), provides no information on such species identity, and is highly dependent on spatial scale of sampling.

In conclusion, RIL can conserve the richness and community composition of tree species at a similar level with primary forest. These positive effects are a co-benefit of RIL, because RIL is primarily a forestry practice to sustainably produce timber. Unfortunately, unregulated selective logging is still common in the tropics (Blaser et al. 2011). If RIL were adopted in much larger areas of natural production forests, a substantial reduction of logging damage on tree assemblage can be expected while timber is sustainably produced. Our results also demonstrated different scale-dependent responses between the two metrics (species richness and community similarity) to logging intensity. We suggest that research on the forest-management adequacy should include several metrics including community similarity at different spatial scales, rather than just evaluating

changes in a single metric relating to species richness at a single spatial scale.

**Acknowledgements**

This work was supported by the Global Environment Research Fund F-071 and D-1006 of the Ministry of the Environment, Japan, to KK. We thank D.K.M. Esther for assisting research plot establishment, M. Poster and D. Joel for tree species identification, R. Ajon and many other persons for assisting field survey, R. Aoyagi, A. Langner and A. Tanaka for remote sensing analysis, P. Lagan for generous support for every aspect. We acknowledge the kind assistance from Sabah Forestry Department and Forest Research Centre, Sabah.

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676 **Table 1** Forest structure and tree species diversity of three to four 0.2-ha
677 plots and one 2-ha plot in primary, reduced-impact logged (RIL), and
678 conventionally logged (CL) forest. Stem density, above-ground biomass
679 (AGB), maximum dbh, basal area, observed number of families, genera
680 and species, and estimated number species (per 70 stems in 0.2-ha plots
681 and per 850 stems in 2-ha plots) are shown. Parentheses indicate values
682 for trees ≥5 cm dbh. Forests sharing the same letters do not differ
683 significantly at $P < 0.05$. Pioneer species: five *Macaranga* species (*M.*
684 *conifera*, *M. gigantea*, *M. hypoleuca*, *M. pearsonii*, *M. bancana*) and two
685 *Croton* species (*C. argyratus*, *C. oblongus*) of Euphorbiaceae, and two
686 Rubiaceae species (*Neolamarckia cadamba*, *Neonauclea* sp.)

| | 0.2-ha plots | | | | | | 2-ha plots | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Primary | | RIL | | CL | | Primary | | RIL | | CL | |
| Stem density (/ha) | 623 | ±97 | 613 | ±72 | 457 | ±85 | 607 | | 504 | | 428 | |
| AGB (Mg/ha) | 499 [a] | ±60 | 341 [a] | ±52 | 163 [b] | ±84 | 378 | | 290 | | 216 | |
| Maximum dbh (cm) | 114 [a] | ±12 | 106 [a] | ±10 | 63 [b] | ±9 | 129 | | 145 | | 92 | |
| Basal area ($m^2$/ha) | | | | | | | | | | | | |
| Total | 41.2 [a] | ±4.6 | 32.7 [a] | ±4.5 | 19.0 [b] | ±7.4 | 34.2 | | 28.6 | | 23.3 | |
| Dipterocarp | 19.9 [a] | ±3.7 | 13.2 [b] | ±3.4 | 5.1 [c] | ±0.8 | 17.6 | | 12.4 | | 8.5 | |
| Pioneer | 1.3 [b] | ±0.5 | 2.3 [b] | ±1.9 | 8.1 [a] | ±3.7 | 0.4 | | 2.4 | | 4.2 | |
| Observed no. families | 30.3 [a] | ±1.9 | 29.0 [a] | ±2.0 | 20.7 [b] | ±2.1 | 52 | (52) | 51 | (53) | 48 | (51) |
| Observed no. genera | 51.5 [a] | ±5.4 | 51.5 [a] | ±4.5 | 30.0 [b] | ±4.6 | 135 | (144) | 124 | (134) | 121 | (131) |
| Observed no. species | 82.5 [a] | ±9.3 | 79.5 [a] | ±10.3 | 39.3 [b] | ±6.4 | 296 | (319) | 298 | (340) | 243 | (263) |
| Estimated no. species | 50.1 [a] | ±9.1 | 49.5 [a] | ±5.9 | 31.1 [b] | ±6.3 | 257 | | 282 | | 243 | |

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688 **Table 2** PERMANOVA test results for community-composition
689 differences between primary, reduced-impact logged (RIL) and
690 conventionally logged (CL) forest. The $r^2$ values are shown for all
691 pairwise comparisons between forest types. Significant differences are in
692 bold. $P$ = * < 0.05, ** < 0.01, *** < 0.001
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| | 0.2-ha plots | 2-ha plots |
|---|---|---|
| Among the three forests | **0.19** ** | **0.35** *** |
| Primary-RIL | 0.15 | **0.31** *** |
| Primary-CL | **0.31** * | **0.39** *** |
| RIL-CL | **0.36** * | **0.18** *** |

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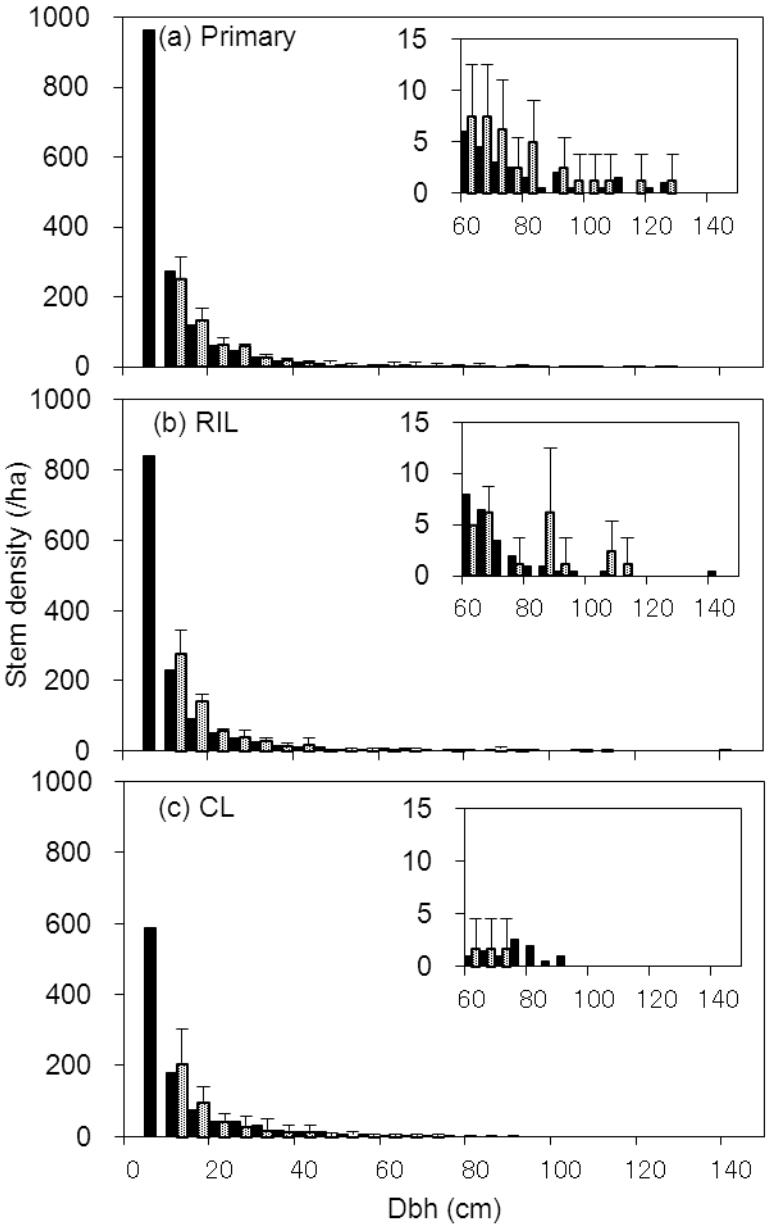
## Figure captions

**Fig. 1** Frequency distribution of dbh for trees ≥ 5 cm dbh at one 2-ha plot (black bars) and trees ≥ 10 cm dbh at three to four 0.2-ha plots (dotted bars) in primary (a), reduced-impact logged (RIL) (b) and conventionally logged (CL) forest (c). Values for trees ≥60 cm dbh are also shown in an inlet. Error bars indicate SD.

**Fig. 2** An ordination of tree community composition of primary, reduced-impact logged (RIL) and conventionally logged (CL) forest in the eleven 0.2-ha plots (a) and thirty 0.2-ha subplots in the three 2-ha plots (b) on the coordinate of axis 1 and axis 2 of NMDS analysis. Stress values are also shown.

**Fig. 3** Species accumulation curves of three to four 0.2-ha plots (a-f) and one 2-ha plot (g-n) in each of primary, reduced-impact logged (RIL) and conventionally logged (CL) forest by tree size class. Error bars indicate SD. Species-area curves: a-c,g-j; species-individual curves: d-f,k-n

**Fig. 4** Relationships between above-ground biomass (AGB) and estimated number of species (a-c) and NMDS axis 1 scores (d-f) in the three sampling designs; three to four 0.2-ha plots and a 2-ha plot in primary, reduced-impact logged (RIL) and conventionally logged (CL) forest, and ten 0.2-ha subplots within each 2-ha plot. Relationships significant at $P < 0.05$ only are shown.

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735 Fig. 1

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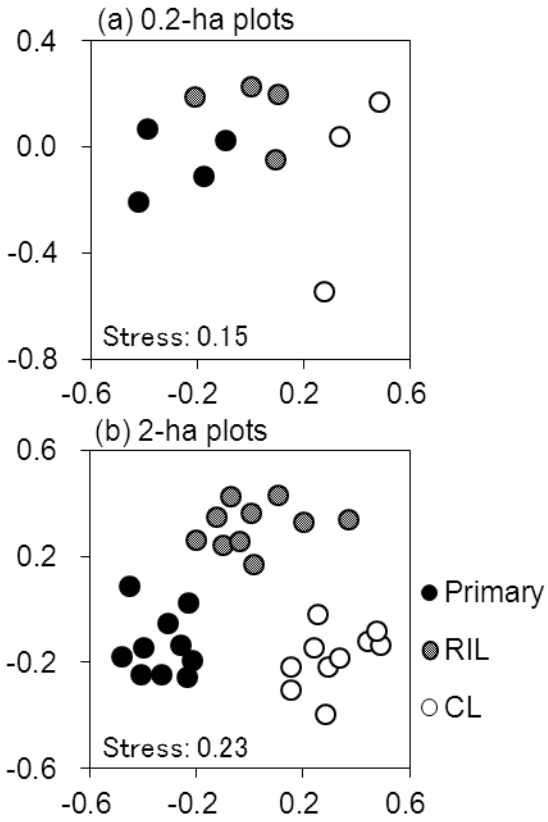


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739 Fig. 2

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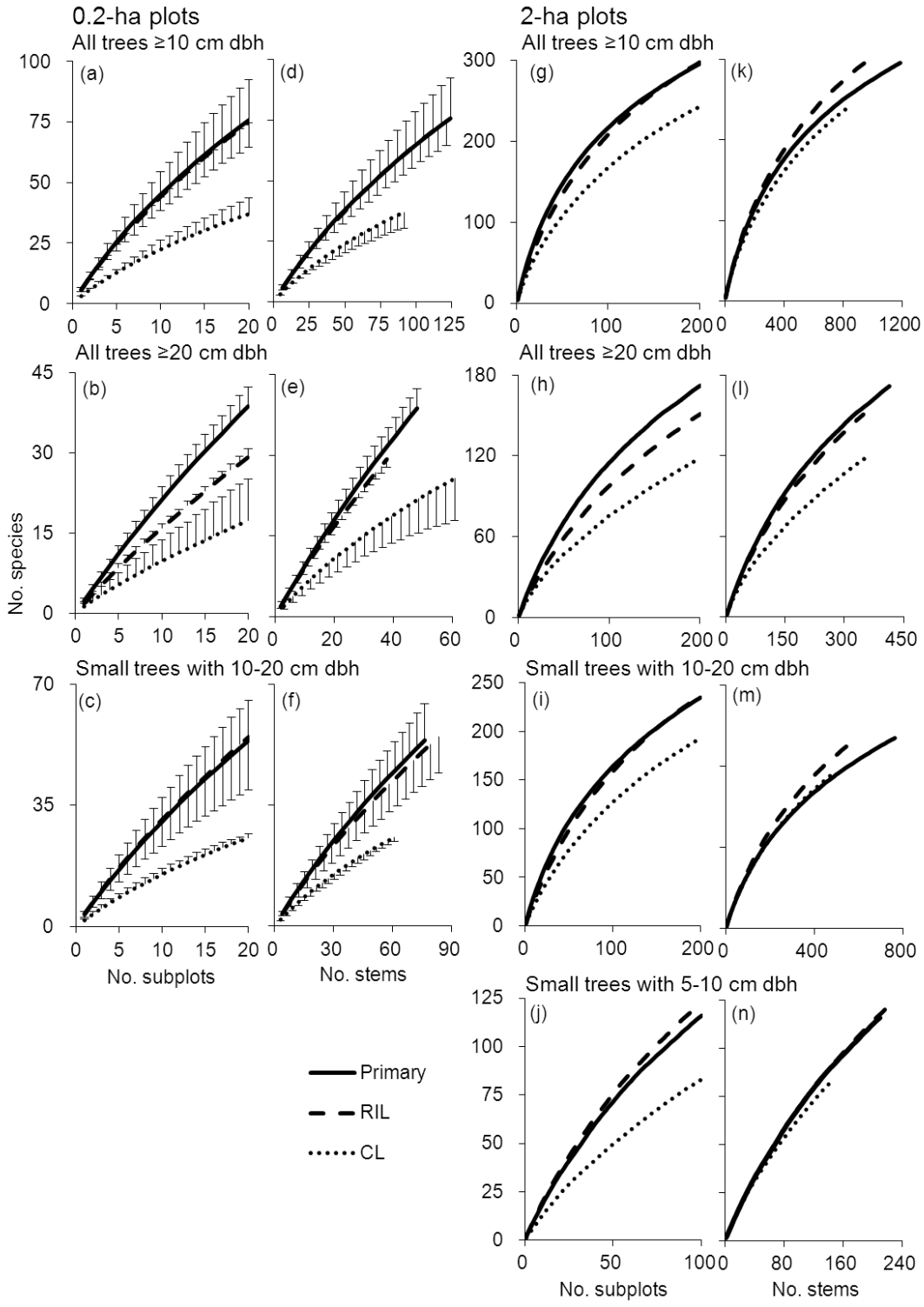


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743 Fig. 3

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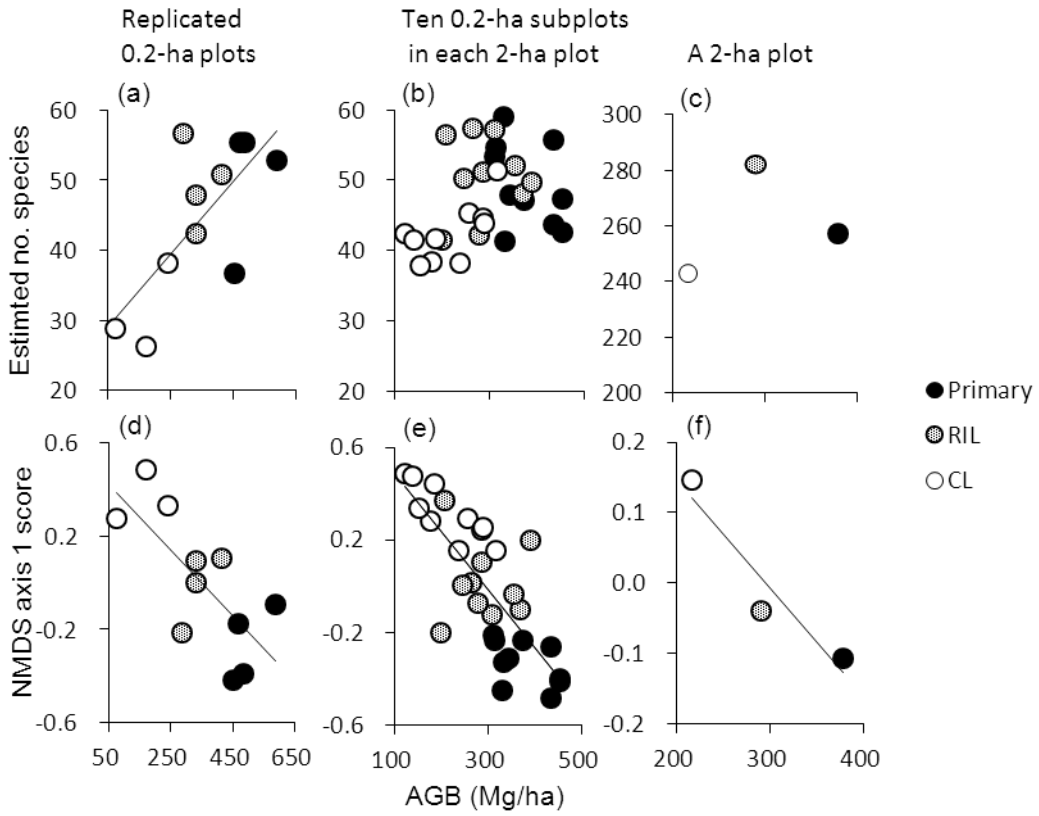


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747 Fig. 4